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Changes in feeding behavior of longfin squid (*Doryteuthis pealeii*) during laboratory exposure to pile driving noise

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ABSTRACT

Anthropogenic noise can cause diverse changes in animals' behaviors, but effects on feeding behaviors are understudied, especially for key invertebrate taxa. With the offshore wind industry expanding, concern exists regarding potential impacts of pile driving noise on squid and other commercially and ecologically vital taxa. We investigated changes in feeding and alarm (defense) behaviors of squid, *Doryteuthis pealeii,* predating on killifish, *Fundulus heteroclitus,* during playbacks of pile driving noise recorded from wind farm construction within squids' habitat. Fewer squid captured killifish during noise exposure compared to controls. Squid had more failed predation attempts when noise was started during predation sequences. Alarm responses to noise were similar whether or not squid were hunting killifish, indicating similar vigilance to threat stimuli in these contexts. Additionally, novel hearing measurements on *F. heteroclitus* confirmed they could detect the noise. These results indicate noise can disrupt feeding behaviors of a key invertebrate species, and will leverage future studies on how noise may disrupt squids' vital ecological interactions.

1. Introduction

Underwater noise from anthropogenic activities has increased in past decades in many areas of the oceans, and accordingly, concern has grown regarding impacts of anthropogenic noise pollution on marine taxa (Andrew et al., 2011; Frisk, 2012; Gedamke et al., 2016; Haver et al., 2017; McDonald et al., 2006; Miksis-Olds et al., 2013). Increased anthropogenic activities such as shipping, seismic surveys for oil and gas exploration, and marine construction all contribute to noise pollution that can harm the physiology and behavior of marine fauna (Gedamke et al., 2016; Hawkins et al., 2015; Slabbekoorn et al., 2010). Noise-related impacts have been noted from crustaceans to cetaceans, although fewer studies have addressed invertebrates compared to vertebrates (Gedamke et al., 2016; Kastelein et al., 2016; Wale et al., 2013a). Noise can interfere with key ecological functions such as predator and prey detection, communication, and navigation (Hawkins et al., 2015; Putland et al., 2019; Stanley et al., 2017).

Impact pile driving is one such noise source of concern in marine environments. This impulsive sound arises from repeated hammer strikes that drive long piles into the seabed. These piles support foundations for coastal docks, piers, and boat slips, and offshore energy platforms such as wind farms. As the offshore wind industry expands globally (Musial et al., 2019), regulatory agencies and fishers aim to predict impacts of wind farm construction on commercially and ecologically important marine fauna. Many offshore wind projects utilize impact pile driving to install turbine supports, typically in waters less than 60 m deep, including the North Sea and the Northwest Atlantic continental shelf (Musial et al., 2019). Underwater sounds from offshore pile driving are high-amplitude, with peak sound pressure levels typically exceeding 200 dB within a range of several-hundred meters from

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the pile (Bailey et al., 2010; S. Lippert and von Estorff, 2014, 2019). Pile driving sounds are also broadband, spanning frequencies from <100 Hz to >10000 Hz, with peak energy usually between 100 and 2000 Hz. These sound are far-propagating, typically detectable by hydrophones well over 10 km away (Amaral et al., 2018; Bailey et al., 2010). As a pile is driven, acoustic waves radiate out from the pile via multiple paths through the water column and substrate (Reinhall and Dahl, 2011); therefore, benthic and interstitial animals as well as animals occupying the water column will be exposed to this noise (Roberts and Elliott, 2017).

Pile driving sounds can have a wide variety of impacts on marine taxa. For example, they can damage organs of fishes (Casper et al., 2013a,b; Halvorsen et al., 2011), and cause temporary reductions in hearing sensitivity, as observed in harbor porpoises and the harbor seal *Phoca vitulina* (Kastelein et al., 2016, 2018). Behavioral changes caused by impulsive anthropogenic noise (including, but not limited to pile driving) are diverse, and include directional swimming responses of fishes and mammals away from the noise source (Aarts et al., 2018; Graham et al., 2019; Mueller-Blenkle et al., 2010), alarm responses (e.g. startle and escape behaviors) and changes in fishes' schooling behaviors, which are important defenses against predators (Hawkins et al., 2014; Herbert-Read et al., 2017; Neo et al., 2015).

Relatively few studies have investigated changes in aquatic animals' feeding and foraging behavior during noise. Sustained reductions in animals' feeding behaviors due to anthropogenic stressors could lead to reduced survival, especially in regions with patchy prey distribution or limited prey abundance. Some studies have reported reduced foraging activity of marine mammals during pile driving, sonar, and vessel noise (e.g., Aarts et al., 2018; Erbe et al., 2019; Miller et al., 2015). In studies on fishes and invertebrates, exposure to boat noise and white noise has resulted in reduced prey capture rate, increased food handling or discrimination error, and decreased time spent foraging (e.g., Ivanova et al., 2020; Mensinger et al., 2018; Purser and Radford, 2011; Sabet et al., 2015). While the vast majority of studies on feeding behaviors during noise have focused on marine mammals or fishes, comparatively few have focused on marine invertebrate taxa, despite a growing number of invertebrates known to detect acoustic cues (Carroll et al., 2017; Popper and Hawkins, 2018; Samson et al., 2016) and their high biomass and central ecological role in ocean ecosystems (Costello et al., 2010). Cephalopods (squids, cuttlefishes, and octopuses) comprise an estimated 20% of global fishery landings and values (Hunsicker et al., 2010) and are a key trophic link between many top predators, and smaller fish and invertebrate prey (Boyle and Rodhouse, 2005; Hanlon and Messenger, 2018). They are also considered sound-sensitive, demonstrating neural and behavioral responses to sounds below 1000 Hz (Kaifu et al., 2008; Mooney et al., 2010; Packard et al., 1990). The ecological functions of their hearing abilities remain elusive; hypothesized uses of natural sounds include prey detection, predator avoidance and navigation (Samson et al., 2016; Wilson et al., 2018). Their low-frequency hearing range overlaps with dominant frequencies of many anthropogenic noise sources, including pile driving (Slabbekoorn et al., 2010). Cephalopods are therefore at risk for noise-induced changes in hearing physiology and behavior, as has been demonstrated in a few studies.

Though studies investigating effects of anthropogenic noise on invertebrates' feeding behavior are limited, several studies have indicated adverse effects of anthropogenic noise on other behaviors, and physiology of cephalopods and other invertebrate taxa. Hair cells in hearing structures of the cuttlefish *Sepia officinalis*, and squids *Loligo vulgaris* and *Illex coindetii* suffered damage after 2 h continuous exposures of noise (Solé et al., 2017, 2018, 2019). Southern reef squid, *Sepioteuthis australis*, exhibited alarm responses, i.e., inking and jetting, during impulsive air gun noise (Fewtrell and McCauley, 2012). Pile driving noise in a prior laboratory study elicited alarm responses in longfin squid, *Doryteuthis pealeii*, including inking, jetting, and body pattern changes (Jones et al., 2020). Rock lobsters, *Jasus edwardsii*, exposed to air gun noise had an impaired behavioral righting reflex (employed to escape predation), and had damage to statocyst structures important in controlling this righting response (Day et al., 2019). Further, bay scallops, *Pecten fumatus*, exposed to air gun noise had higher mortality rates, higher rates of recessing behavior, and changes in haemolymph biochemistry suggestive of reduced capacity for homeostasis (Day et al., 2017). These studies indicate diverse potential noise impacts on cephalopods and other invertebrates, though the extent of impacts on these taxa are only just beginning to be understood.

The current study focused on the longfin squid, *Doryteuthis pealeii*, which inhabits continental shelf waters in the Western Atlantic Ocean, ranging from Venezuela to Newfoundland. The species is most abundant in the Northeast U.S., between Cape Hatteras, NC, and Georges Bank (Hanlon et al., 2013). In that region, offshore wind farms are planned for construction in the 2020s and 2030s within 18 established lease areas (Musial et al., 2019). Longfin squid are commercially important, with average annual landings of about 11,000 mt and values of $30 million since 2010 (NMFS, 2020). They are opportunistic predators that feed on a wide variety of fish and invertebrate species throughout their lifetime (Hunsicker and Essington, 2006; Vovk, 1985). Small, young juveniles feed primarily on copepods, and they consume increasingly larger fish prey as they grow into adults. Squid rely heavily on visual cues for communication and finding prey, and are more likely to pursue mobile prey than stationary prey (Hanlon and Messenger, 2018). Longfin squid are known to feed during the daytime and at night (Macy, 1982; Vovk, 1985). They have fast metabolisms, rapid digestion rates, and limited energy stores; thus it is suspected they need to frequently consume prey to survive in the wild (Hanlon et al., 2013; Hatfield et al., 2001).

In the present study, we examined how playbacks of sounds from impact pile driving influenced predation by the ecologically key squid *D. pealeii*. In both daytime and nighttime trials, live killifish, *Fundulus heteroclitus*, were added to the experimental tank to quantify squids' prey capture rates, failed predation attempts, and latencies to predation behaviors. We also quantified the mobility level of the killifish as a potential covariate in squid feeding behaviors, and we measured the hearing range of *F. heteroclitus* using neurophysiological auditory evoked potential (AEP) methods to assess their ability to detect the sounds. This study intends to elucidate how pile driving noise may alter feeding behaviors critical for individual squid's survival.

2. Materials and methods

Experiments during the daytime ("Day" trials) were conducted between June 23 and July 27, 2018 (n = 54 trials). Experiments during the nighttime ("Night" trials) were conducted between September 4 and October 21, 2018 (n = 32 trials). Day trials took place during daylight (between 09:00 and 18:45 local time), and Night trials took place after astronomical twilight (between 20:00 and 02:45 local time).

2.1. Animal collection and care

Squid were collected from Vineyard Sound (41° 22′ N; 70° 47' W) via trawls conducted by the Marine Biological Laboratory (Woods Hole, MA). Recently trawled squid were transported in seawater-filled coolers to flowing-seawater facilities at Woods Hole Oceanographic Institution (WHOI; Woods Hole, MA). At WHOI, prior to experiments squid were held for 1–4 days in a semi-outdoor tented building in cylindrical holding tanks at least 1.2 m in diameter and with 0.8 m water depth (900 L) with ambient flowing seawater. The water temperature of these holding tanks was 21.7 ± 0.9 °C (mean ± SD) from June to July and 19.0 ± 1.5 °C from September to October, and they were subject to the natural light cycle. Squid sharing a tank were same-sex and of similar size, to minimize damage to squid due to aggression, and densities were kept no higher than one squid per 225 L. Squid were fed every evening (16:00–19:00 local time) with killifish, *Fundulus* sp., (WHOI IACUC approval to TAM) collected from local estuaries.

2.2. Experimental tank setup

Experiments took place in a 1.1 m diameter cylindrical tank, filled to 0.5 m depth with ambient flowing seawater (Fig. 1). An Aqua-30 speaker (Theunissen Technical Trading, Malden, The Netherlands; frequency response: 100 Hz–10 kHz) was suspended, facing horizontally, at 25 cm depth and 15 cm forward of the closest tank wall. The speaker was connected to a PLA-2378 amplifier (Pyle Audio, Brooklyn, NY) powered by a 12 V battery. Audio files were played from a laptop connected to the amplifier. To monitor ambient tank sounds and noise playbacks during experiments, a hydrophone (HTI-96-MIN; High-Tech Inc., Long Beach, MS; frequency response: 2 Hz–30 kHz) was placed 2 cm from the tank wall, 44 cm horizontally from the speaker, and 35 cm deep. This hydrophone was attached either to a SongMeter 2 (Wildlife Acoustics, Maynard, MA) or (due to equipment failure) a SoundTrap ST4300 (Ocean Instruments, New Zealand). An overhead Sony video camera (for Day trials: model HDR-CX440; for Night trials: model HDR-XR550) was used for all video analyses. A small PVC pipe cap with mesh over its bottom opening was used to hold an individual killifish in the tank until the experiment began. A rope was attached to the cap so the experimenter, out of view of the squid, could pull the cap up to reveal the fish. The water temperature of the experimental tank was 22.1 ± 0.7 °C for Day trials and, due to technical difficulties in efforts to heat tank water, temperatures were lower for Night trials: 16.1 ± 1.9 °C (mean ± SD). Squid generally increase their feeding rate and energy consumption with increased temperature, and feeding rates may be doubled with an increase in 10 °C, at least when prey are readily available (Boyle and Rodhouse, 2005; O'Dor et al., 1980). Additionally, feeding habits of wild longfin squid may vary seasonally (Macy, 1982; Vovk, 1985). Due to the temperature and seasonal differences of Night trials from Day trials, Night trials were analyzed separately from Day trials, and comparisons between the two datasets are not made. Differences between holding tank temperatures and experimental tank temperatures at the time squid were transferred between these tanks were 0.6 ± 0.6 °C for Day trials, and 3.0 ± 1.9 °C for Night trials.

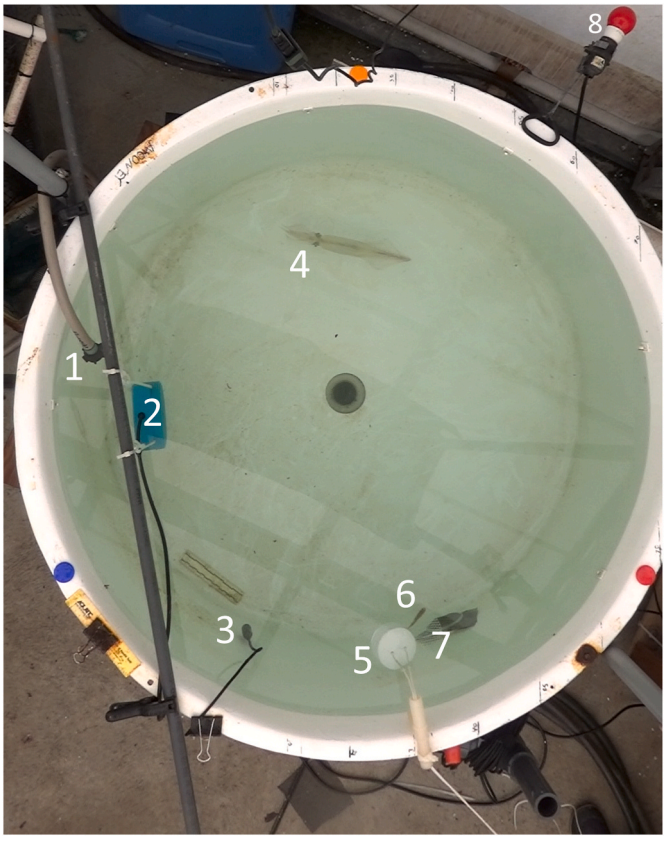

Fig. 1. View of experiment tank from top-down video camera. 1) Inflow hose, 2) underwater speaker (Aqua-30), 3) hydrophone to monitor ambient sound and playbacks during experiments, 4) squid (*Doryteuthis pealeii*) 5) PVC container lifted to reveal fish, 6) fish prey (*Fundulus heteroclitus*), 7) flow outlet, covered with mesh, 8) LED to indicate start of playbacks (used only in Day trials). The dark circle in the center of the tank is a plugged outflow pipe.

For Night trials only, black tarps were hung around the experimental tank to block out lights from playback equipment and the video monitor, and a U6R infrared light (Univivi, China; 850 nm wavelength) above the tank provided illumination for the camera, which was set to 'night mode' (similar to York et al., 2016). Visual photoreceptors of *D. pealeii* contain only one pigment, which has peak sensitivity at 493 nm (Hara and Hara, 1976), well below the wavelength of the infrared light.

2.3. Audio playback files

Audio files of pile driving sounds used for the experiments were recorded during construction of the Block Island Wind Farm (BIWF, Rhode Island, USA) on October 25th, 2015, at 19:38 UTC, from a hydrophone (HTI-94-SSQ, High Tech Inc., sensitivity: 203.8 dB re 1 V/μPa, gain: 6 dB, flat frequency response from 2 Hz to 30 kHz) on a benthic sled 26 m deep and 500 m away from a pile driving site, and about 1 m above the seabed (Amaral et al., 2018). Files were recorded at a 9766 Hz sample rate. These data were provided to the authors (see Acknowledgements). The time interval between pile strikes was 1.8 s. The steel, hollow pile had a diameter of 127.0 cm, wall thickness of 3.8 cm, a rake of 13.27° with respect to vertical, and was driven up to 76.2 m deep into the seabed.

To avoid pseudoreplication of playback stimuli, three 10-min long recordings were generated from one pile driving bout and edited in Adobe Audition (Adobe Systems, San Jose, CA) prior to playback. The files consisted of a 1-min sequence of pile strikes with a randomized order of pile strikes, and this sequence was repeated for a total file length of 10 min. The intervals between all pulses were edited to be 2 s long. The recordings were amplified by a custom magnitude to obtain the highest playback sound levels possible without clipping, with the goal to match received sound pressure levels in the tank with those present 0.5 km from the BIWF pile driving site, i.e. 190–194 dB re 1 μPa (zero-to-peak). For Control trials, a 10-min long silent file was played, to account for potential influences of the powered playback system's electrical field.

2.4. Experimental procedure

Only healthy squid (i.e., those without large skin lesions and with normal feeding behavior, having eaten a killifish the prior day) were selected for experiments (mantle length 8.5–23.0 cm, mean ± SD: 15.5 ± 3.0 cm). At the start of an experiment on a given squid, approximately 24 h had elapsed since the squid last ate, so they were more likely motivated to feed during the experiment (Bidder, 1950). Each trial used a different squid; individuals were not retested. At the start of a trial, a killifish (total length 3.5–8.0 cm, mean ± SD: 5.2 ± 1.2 cm) was placed in the PVC cap in the experimental tank prior to adding the squid. The range in body length of prey that squid consume positively correlates with squid mantle length (Vovk, 1985), and we took care to scale the length of killifish added with squid length for each trial. Hydrophone and video recording began just after squid were transferred to the experimental tank. Squid were acclimated to the tank for at least 10 min prior to starting an experiment, until squid were consistently swimming back-and-forth in the middle of the tank and not interacting with the tank walls. As determined in prior studies, 10 min was sufficient time for these squid to return to this 'normal' in-tank behavior after transfer to a new tank (Jones et al., 2020; Mooney et al., 2016).

There were three playback treatment types, designated "Onset", "5min", and "Control". Treatment was randomly selected for each trial.

In Onset trials, the experimenter raised the PVC cap to reveal the killifish prey after the acclimation period, and waited for the squid to start pursuing it, at which time the pile driving noise was immediately started. The noise exposure lasted for 10 min or until the squid captured and began consuming the fish. In 5min trials, the pile driving playback was started after the acclimation period but 5 min before the fish was revealed. After revealing the fish, the playback continued for five more minutes or until the squid captured and began consuming the fish. Control trials had the same protocol as Onset trials, except that a 10-min long silent file was played instead of the pile driving noise file. For all trials, if the squid did not pursue the fish within 10 min after the fish was revealed, the trial was ended. The noise exposure duration was chosen based on observations of squid in preliminary noise trials that consumed prey less than 10 min, often within 1 min, after its reveal. Though durations of individual pile driving periods are variable in the field, this experimental duration was within the range of those observed for BIWF construction (Amaral et al., 2018). A summary of sample sizes is presented in Table 1.

2.5. Acoustic calibration of the experimental tank

Recordings of the sound field in the experimental tank followed methods and instrumentation used in Jones et al. (2020), and are briefly described here. The experimental tank was calibrated in 10 cm increments in all three dimensions (280 positions total) without animals present, creating a 3D array of received sound levels. The same noise file (looped in experiments) was played for 1 min, with the same equipment as in experiments. Cephalopods are thought to detect acoustic particle motion rather than pressure (Budelmann, 1992), and particle acceleration is likely the relevant transduction stimulus (Budelmann and Tu, 1997). Particle acceleration in the tank was recorded with a PCB triaxial accelerometer (model W356B11; frequency response: 0.5 Hz–5 kHz, and sound pressure was recorded with a Reson TC4013 hydrophone (frequency response: 1 Hz–170 kHz) for ease of comparison with other studies.

2.6. Acoustic data analyses

Acoustic data analyses were conducted following methods described in detail in Jones et al. (2020). Briefly, zero-to-peak levels of individual pile impulses were calculated, in dB for sound pressure ($SPL_{z\text{-}pk}$) and particle acceleration ($SAL_{z\text{-}pk}$) as follows:

$$SPL_{z-pk} \text{ or } SAL_{z-pk} = 20^{*}Log_{10}\left(X_{pk}\right)$$

where X_{pk} is the maximum absolute μPa or μm s^{-2}. For simplicity, the 3D norm of particle acceleration (a vector quantity) was calculated and its magnitude is reported. Power spectral density (PSD) was calculated as described in Jones et al. (2020). All acoustic analyses were limited to a 20–1000 Hz frequency range.

Table 1
Number of trials conducted for each of the six treatments. The first number is the total number of trials attempted, including both trials without playback and those with playback, and is the sample size for the analysis reported in Fig. 3B (Day) and 4B (Night). The second number (in parentheses) is the number of trials with playback, and is the sample size for analysis reported in Fig. 3A (Day) and 4A (Night). Results reported in Fig. 5, and 7–9 have sample sizes subset from numbers in parentheses here, according to conditions specified in their associated figure captions and text. . Note that by experimental design, playback occurred in every '5min' trial, and playback was not started in Control or Onset trials if squid did not pursue the prey.

	Day	Night	Total
Onset	18 (13)	10 (6)	28 (19)
5min	20 (20)	12 (12)	32 (32)
Control	16 (15)	10 (5)	26 (20)
Total	54 (48)	32 (23)	86 (71)

2.7. Behavior data analyses

The squids' feeding behaviors were classified into three groups: 'no attempt', if the squid made no predation attempt (no pursuit or attack behaviors); 'failed attempt', if squid had at least one failed predation attempt (a pursuit or attack that did not result in successful fish capture) and no subsequent capture; and 'capture', if the squid successfully captured and began ingesting the fish (some of these squid had failed attempts beforehand). One squid in the Day Control treatment captured then immediately released the fish within 1 s, and did not recapture the fish during the trial, thus was placed in the 'failed attempt' category. To compare proportions of squid with these outcomes across treatment types, 2 × 2 Fisher's Exact tests were performed (expected counts were too low to perform chi-square tests). Importantly, by experimental design, when limiting analyses to trials only in which a playback file was started, no squid in the Control and Onset treatments could belong to the 'no attempt' category since playback was only started if the squid pursued the fish. The proportion of squid that made no attempt to capture the fish in 5min trials may include squid that were not motivated to feed during the time of experimentation, i.e., they may have similarly not pursued the fish if they were tested in Onset or Control trials. Therefore, statistical comparisons of capture rates among trials with audio playback were made only between Control and Onset treatments.

The number of failed predation attempts was also tracked, among a subset of trials that met two criteria: 1) a silent or pile driving playback was started, and 2) the squid made at least one predation attempt. Squid that captured the fish on their first predation sequence were assigned a failed attempt count of zero. These data were not normally distributed, thus Kruskal-Wallis tests and pairwise Mann-Whitney U (MWU) tests were used to compare the median number of failed predation attempts across treatment types. The time from when the killifish prey was revealed to when the squid first exhibited each of the four predation sequence stages (orient, pursuit, attack, capture) was quantified, hereafter referred to as 'predation latency', and was tested for statistical differences across treatment types with Kruskal-Wallis tests. Due to lower sample sizes for the 'Night' dataset, this analysis was only performed on the 'Day' dataset.

The locomotion of the killifish during trials was quantified as the proportion of the time the killifish spent swimming, and analyzed as a potential covariate of predation latency. 'Swimming' was defined as translational movement, as opposed to finning or pivoting in one location. Killifish swimming was quantified in 2 s time bins from the time the fish was revealed to the time it was captured, or until 5 min elapsed, whichever came first. These data were log-transformed to reach an approximately normal distribution, for use in linear regression analyses and analysis-of-covariance (ANCOVA). Again, due to lower sample sizes for the 'Night' dataset, this analysis was only performed on the 'Day' dataset.

Squid alarm responses, including inking, jetting, startle responses, and body pattern changes were also quantified. These behaviors were depicted and their ecological functions described in detail in Hanlon et al. (1999); criteria for their classification can be found in Jones et al. (2020). We chose to focus on alarm responses naturally employed by squid as anti-predator defense behaviors. Inking refers to the release of ink, jetting is a fast, backwards propulsive escape response, and startle responses are sudden locomotor movements other than jetting. Body pattern changes are changes in the color and pattern of a squid's skin via specialized organs (chromatophores) and cells (e.g. iridophores). Body pattern changes are expressed to startle, bluff, or distract predators, and to communicate with conspecifics. We sought to compare alarm response rates when squid were hunting killifish at the start of noise (Onset trials) to those rates when the killifish was hidden from the squid (5min trials) to see if the presence of prey and active hunting behavior altered these response rates. These analyses were similar to those from a

prior study analyzing alarm responses in the same experimental setup but not in a feeding context (Jones et al., 2020). In that previous study, nearly all alarm responses occurred during the first minute of playback. Thus, analyses of alarm behaviors during playback periods in the present study focused on the first minute of playback. Inking, startle behaviors, and body pattern changes were difficult to observe from video in Night trials, thus most analyses of alarm responses were limited to Day trials, and only jetting was analyzed in Night trials. Alarm response rates were quantified and compared in three ways: 1) between the last minute preceding the start of noise or Control playbacks (pre-playback period) and the first minute of the playback period (Fisher's Exact tests), 2) during the first minute of playback among the three playback treatment types (Fisher's Exact tests), and 3) per pile impulse (quasipoisson GLMs).

Whenever multiple pairwise tests (either Fisher's Exact or MWU) were performed to compare the playback treatments (three comparisons), the Holm's sequential procedure was used to determine significance thresholds (α). Holm's is a modification of the Bonferroni procedure, and is just as effective at controlling for type I error, but reduces the likelihood of type II error (Eichstaedt et al., 2013). Briefly, this involves first performing each comparison, then ordering resulting p values from smallest to largest. The comparison with the lowest p value is tested with a Bonferroni adjustment for all other comparisons, in our case at $\alpha = 0.0167$. The comparison with the second lowest p value is tested with a Bonferroni adjustment for one fewer test, in our case at $\alpha = 0.025$, and so on, so our third comparison is tested at $\alpha = 0.05$. The procedure stops at the first non-rejection of the null hypothesis.

2.8. *Fundulus heteroclitus* auditory evoked potentials (AEPs)

The AEP method was used to determine the general hearing range of *F. heteroclitus*. This method records electrical responses of groups of auditory nuclei in the brainstem and eighth cranial nerve of fishes. Tonal stimuli are played to determine minimum response thresholds at multiple individual frequencies. The goal was to determine the species' hearing thresholds and range of sound sensitivity, and place these data in context with the frequency spectrum of pile driving noise played to killifish during experimentation. Killifish not used in feeding trials were used for these hearing tests (n = 6, mean ± SD of total length: 9.0 ± 0.4 cm). One additional, dead control fish (total length: 10.0 cm) was measured to confirm responses recorded in live fish were of neural origin and not artifacts of the recording and playback system.

The experimental setup, recording, and calibration procedures were similar to those of Stanley et al. (2020), and are described in detail in the present study's Supplementary Info. Briefly, fish were anesthetized in a dilute solution of 100% clove oil (0.25 mL clove oil: 1 L seawater) to reduce large muscular movements. Fish were then placed in a 0.95 × 0.6 × 0.7 m (length, width, depth) PVC tank with a seawater temperature of 7.7 ± 0.3 °C (mean ± SD), and subdermal electrodes were inserted to measure neural responses. Auditory stimuli were generated using custom LABVIEW software (National Instruments) on a laptop (S6520 Lifebook S, Fujitsu), and were played through an underwater speaker (UW-30) in the tank. Stimuli were sinusoidal amplitude-modulated tone pips presented at 80, 100, 150, 200, 300, 400, 600, and 800 Hz, in a random order. Stimuli were presented at a given frequency in decreasing amplitude until a response could no longer be seen in the recording waveform, then attenuated 5–10 dB further to ensure minimum response thresholds were reached. Auditory thresholds were determined by visual inspection of waveforms, whereby the lowest sound level at which a clear response was detected was taken as the threshold.

3. Results

3.1. Experimental acoustic field

The confines of the tank provided a quiet and isolated background environment for the study. Pressure spectra of ambient sound in the tank were at least 30 dB lower than those of the pile driving noise, and spectral levels of the silent Control playbacks were similar to these ambient levels. Accelerometer recordings of ambient sound and silent playbacks resulted in flat spectra at the self-noise floor of the accelerometer, i.e. 55 dB re 1 μm s^{-2} (not shown), thus these conditions were likely at lower acceleration levels.

$SAL_{z\text{-}pk}$ and $SPL_{z\text{-}pk}$ of the pile driving playbacks were highly variable throughout the tank, ranging from about 130 to 150 dB re 1 μm s^{-2} and 160–180 dB re 1 μPa, respectively (Fig. 2A). For both metrics, amplitudes were more variable in the horizontal plane than across depths, though generally, higher amplitudes were recorded at 20 and 30 cm depths than at 10 and 40 cm depths. Particle acceleration followed a complex, non-monotonic pattern with distance from the speaker. Sound pressure was higher closer to the speaker and dropped off with distance from the speaker along the X and Y axes, increasing again near the tank boundaries. Acceleration PSD in the tank exceeded that recorded in the field, by up to 40 dB at frequencies below 400 Hz (Fig. 2B). Pressure spectra of noise pulses in the tank were generally lower than, and within 30 dB of PSD of the field recordings (Fig. 2C). Below 400 Hz, the pressure spectra of pulses in the tank were closer to those in the field, generally within 20 dB. The reader is referred to Jones et al. (2019) for a more detailed description of these tank calibration data and acoustic propagation in the tank used for the present study.

3.2. Prey capture rates: 'day' trials

The proportion of squid that pursued or attacked fish without capture ('failed attempt') was greater in the Onset treatment, but not significantly so (Fig. 3A). Between Onset and Control treatments, there were no significant differences in rates of 'failed attempt' (odds ratio (OR) = 0.25, 95% confidence interval (CI): 0.04–1.58, p = 0.198) or 'capture' (OR = 4.06, 95% CI: 0.63–26.1, p = 0.198; Fisher's Exact tests). A lower proportion of squid in the 5min treatment captured the prey than in Control and Onset. In 5min trials, some squid made no attempt to pursue or attack the fish ('no attempt'). Note that all squid reported in Fig. 3A were played a pile driving noise or silent Control file.

We sought to compare the proportion of squid that made no predation attempts in the 5min treatment, with that of the other treatments (Fig. 3B). In this analysis, the 'no attempt' category in the Control and Onset treatments defines squid that were likely not motivated to feed in the experiment tank, as these squid did not pursue the fish and were not exposed to any audio playback. Thus a similar 'no attempt' proportion in 5min treatments compared to the Control and Onset treatments suggests squid with 'no attempt' in the 5min treatment were not motivated to feed prior to playback. Conversely, a higher 'no attempt' proportion in the 5min treatments suggests reduction in feeding behavior caused by noise playback. In Day trials, there was no significant difference in the proportion of squid that made 'no attempt' in the 5min treatment, compared to either Control (OR = 0.16, 95% CI: 0.02–1.46, p = 0.104) or Onset (OR = 0.90, 95% CI: 0.21–3.66, p = 1.000; Fisher's Exact tests).

3.3. Prey capture rates: 'night' trials

In the 'Night' dataset, there were similar rates of 'failed attempt' or 'capture' between Onset and Control treatments, though low sample sizes in these treatments, limited to the number of squid that pursued the fish, precluded our ability to perform statistical comparisons (Fig. 4A). Analyzing all Night trials performed, (as done for Day trials in Fig. 3B), the 'no attempt' proportion was similar (40–50%) in Night Control and Night Onset treatments, and was higher (83%) in the Night 5min treatment than the control (though not significantly so: p = 0.074, Fisher's Exact tests) (Fig. 4B).

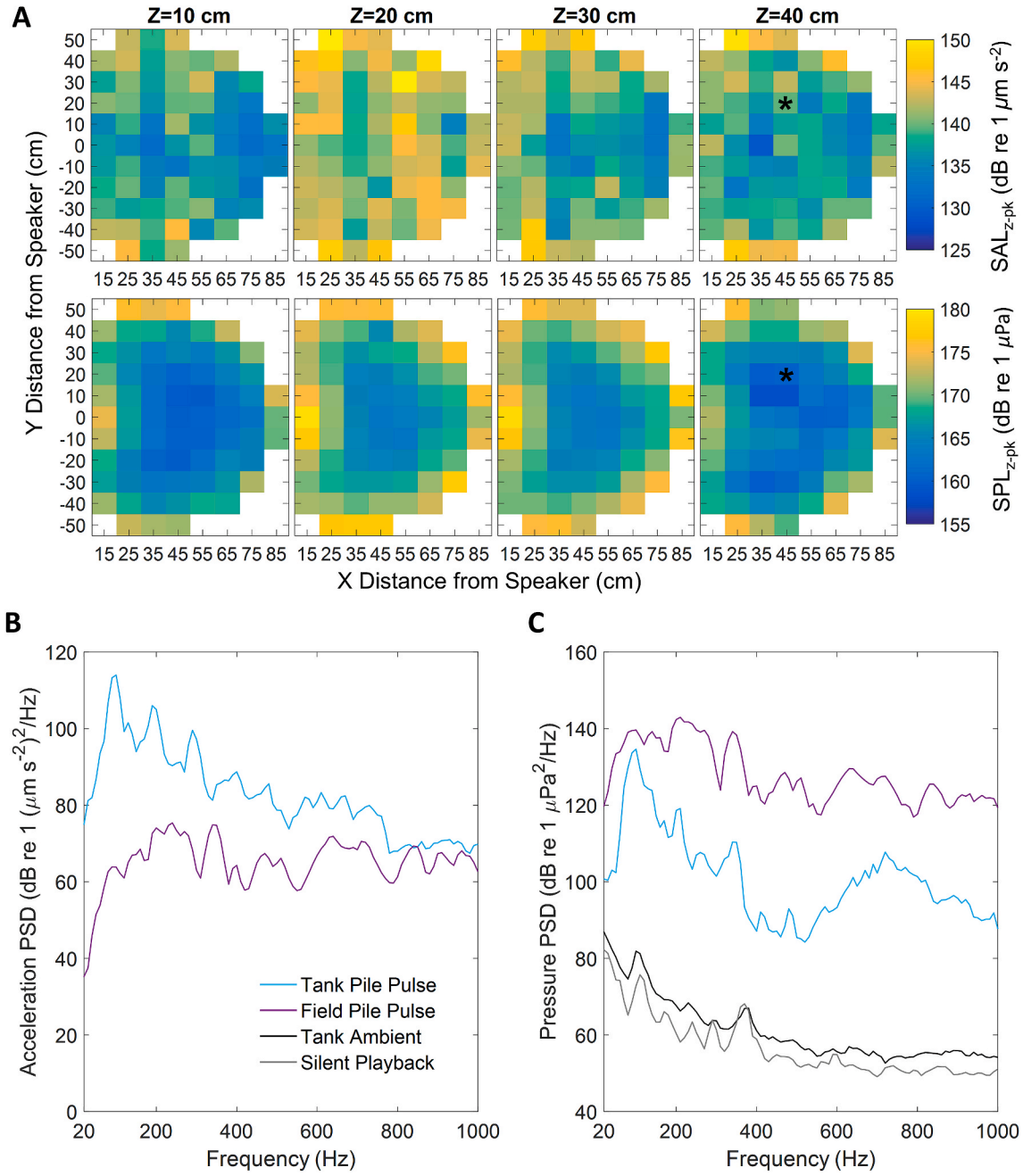

Fig. 2. A) Spatial maps of zero-to-peak acceleration (top) and pressure (bottom) for four water depths (columns), shown from top-down in the horizontal plane, with the front-center of the speaker set as the origin. Data were band-pass filtered to 20–1000 Hz and median zero-to-peak values of pile pulses (across 30 pulses, i.e. 1 min) are shown for each recording location. The asterisks indicate the recording location at which spectra are shown in B and C. Power spectral densities are shown for particle acceleration (B) and sound pressure (C) in time windows covering pile driving pulses of in-tank playbacks and original field recordings. The median spectra of 30 pulses are shown. Spectra of ambient tank sounds (no playback) and the silent playback file are also shown in pressure, but not in acceleration since these conditions were below the noise floor of the accelerometer (see section 3.1).

3.4. Failed predation attempts

The median number of failed attempts was highest for squid in Onset trials (Fig. 5). There were significant differences among the three treatments ($\chi^2 = 8.08$, df = 2, n = 42, p = 0.018; Kruskal-Wallis; Fig. 5). Pairwise tests revealed a significant difference in the median number of failed attempts between Onset and 5min treatments (z = 2.43, U = 138; p = 0.015; MWU with Holm's procedure; lowest p value of the three comparisons), and between Onset and Control treatments (z = −2.36, U = 50, p = 0.018; second lowest p value). The failed attempt rate was statistically similar between squid in Control and 5min treatments (z = 0.39, U = 113, p = 0.697).

In Day Onset trials, 53% of failed attempts stopped at the pursuit stage, and the other 47% of failed attempts were missed attacks (15 total failed attempts). About 83% of failed attempts ended at the pursuit stage and 17% ended at the attack stage in Day 5min trials (6 total failed attempts), and 43% and 43% in Control trials, respectively (7 total failed attempts). The remaining 14% in the Control trials represents one squid that captured then immediately released the fish.

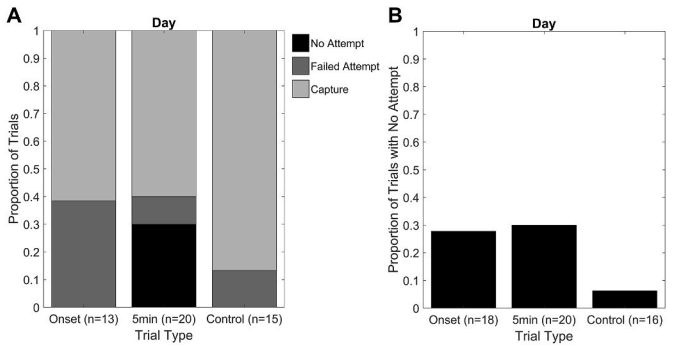

Fig. 3. A) Proportions of trials in the 'Day' dataset, in which squid successfully captured and consumed the fish ('Capture'), attempted to capture (with pursuit and/or attack) but did not successfully capture ('Failed Attempt'), or made no attempt to pursue or capture the fish ('No Attempt') during playback, for each playback treatment. Only trials in which a silent or pile driving playback was started are included here. B) Proportions of squid that made no attempt to feed in the 'Day' dataset. The proportions of 'No Attempt' in Onset and Control treatments represent squid that received no noise exposure or control playback, respectively, as they did not pursue prey during the trial. Sample sizes for Onset and Control treatments are greater than in 3A because trials in which no playback was started are included here. All squid in 5min trials received noise exposure, starting 5 min before the prey was revealed.

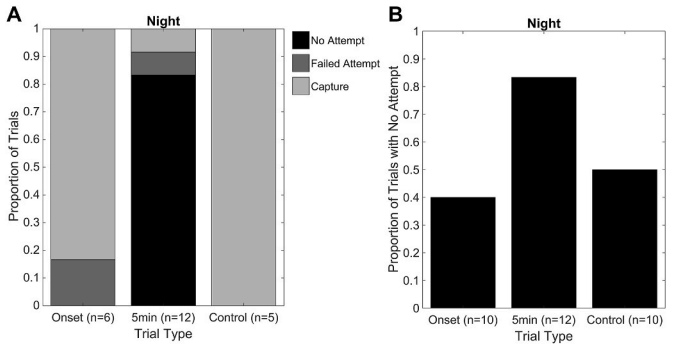

Fig. 4. A) Proportions of trials in the 'Night' dataset for feeding behavior outcomes as detailed in Fig. 3A. Only trials in which a silent or pile driving playback was started are included here. B) Proportions of squid that made no attempt to feed in the 'Night' dataset. The proportions of 'No Attempt' in Onset and Control treatments represent squid that received no noise exposure or control playback, respectively, as they did not pursue prey during the trial. Sample sizes for Onset and Control treatments are greater than in 4A because trials in which no playback was started are included. All squid in 5min trials received noise exposure, starting 5 min before the prey was revealed.

3.5. Predation latency

Comparing the three playback trial types in Day trials, there were no significant differences in the time elapsed from when the fish was revealed to the squids' first display of each predation sequence behavior (orient, pursuit, attack, capture; $p > 0.05$, Kruskal-Wallis tests; Fig. S1; detailed statistics in Table S1). Assessing the three playback treatments together, median latencies for orient, pursuit, attack, capture were 13, 15, 23, and 23 s respectively, with interquartile ranges of 3–37, 4–41, 9–80, and 11–100 s, respectively. Note that here, some sample sizes (see Fig. S1, Table S1) were smaller than those for analyses reported for Fig. 5 because not all squid exhibited all four predation sequence stages.

3.6. Fundulus heteroclitus audiogram and activity levels

Killifish responded to tones played at 80–400 Hz but did not respond to 600 Hz and 800 Hz tones (Fig. 6A). In terms of root-mean-square SPL, killifish had the most sensitive hearing (lowest thresholds) at 200 Hz and reduced sensitivities below and above 200 Hz. Comparison with the frequency spectrum of in-tank pile driving noise playbacks from Fig. 2C indicates the killifish were able to detect the noise, at least at frequencies between 80 and 200 Hz. For comparison, acceleration levels of pile driving noise during the experiment were close to or above squid hearing thresholds (reported in Mooney et al., 2010) from 100 to 300 Hz (Fig. 6B).

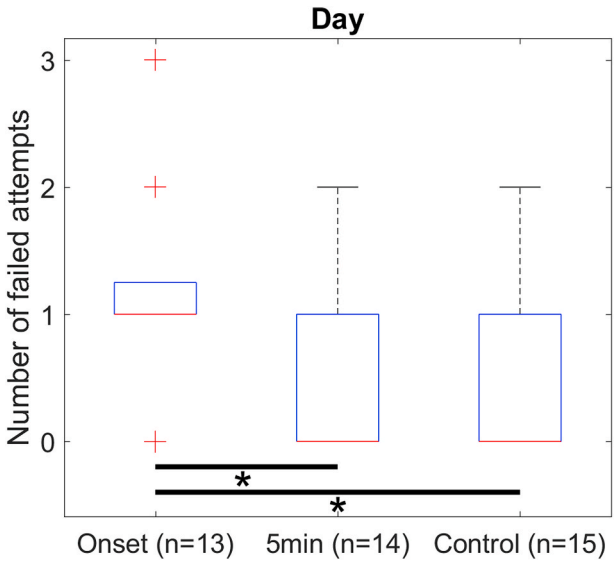

Fig. 5. Number of failed predation attempts (defined as a pursuit and/or attack without capture during a predation sequence) for Day trials. Only trials in which a silent or pile playback was started are shown. Sample sizes are reduced here for the 5min treatment compared to data presented in Fig. 3, because only trials in which squid made at least one predation attempt were included. Squid that captured the fish on their first predation sequence were assigned a failed attempt count of zero. Outliers (crosses) are defined outside the range $q_3 + 1.5 \times (q_3 - q_1)$ and $q_1 - 1.5 \times (q_3 - q_1)$, where q_1 and q_3 are 25th and 75th percentiles, respectively. Medians are at the bottom of each box, and whiskers extend to integer data points furthest from the median that are not outliers. *$p < 0.017$ for Onset vs. 5min, or $p < 0.025$ for Onset vs. Control (Mann-Whitney U tests with Holm's procedure; see section 2.7 for details).

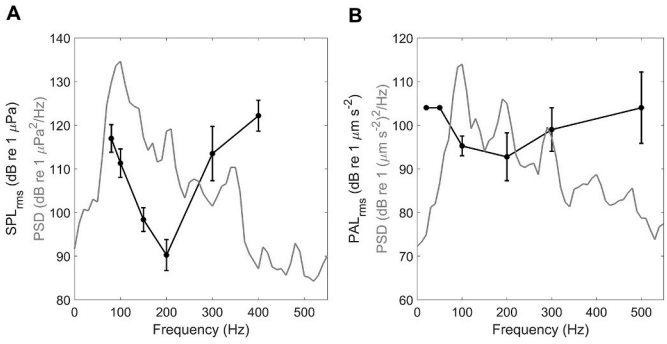

Fig. 6. A) Black line: mean hearing thresholds of *F. heteroclitus* (n = 6 individuals) in terms of root-mean-square sound pressure levels at frequencies from 80 to 400 Hz. No frequencies below 80 Hz were tested, and no responses above 400 Hz were detected (600 Hz and 800 Hz were tested). Grey line: pressure power spectral density (PSD) of pile driving noise in the experimental tank as shown in Fig. 2C. B) Black line: mean hearing thresholds of *D. pealeii* (n = 4 individuals) in terms of root-mean-square particle acceleration levels at frequencies from 20 to 500 Hz, adapted from Mooney et al. (2010). Grey line: particle acceleration PSD of pile driving noise in the experimental tank as shown in Fig. 2B. In A and B, error bars indicate standard deviation of the mean at each frequency.

Killifish mobility levels were correlated with squid predation latencies to address the hypothesis that squid would take more time to predate less mobile prey. The log-transformed time from fish reveal to the first occurrence of each of the four predation stages was negatively correlated with killifish activity levels (Fig. 7). There were significant correlations between prey mobility and log-transformed time to squids' first orient to, attack, and capture of the prey ($R^2 = 0.10$, 0.19, 0.27, and $p = 0.044$, 0.010, 0.003, respectively). One-way ANCOVAs indicated that prey mobility was a significant covariate for the time to first, attack ($df = 1$, $F = 7.60$, $p = 0.010$), and capture ($df = 1$, $F = 9.75$, $p = 0.005$), and not significant for the time to first orient ($df = 1$, $F = 4.09$, $p = 0.051$) and pursuit ($df = 1$, $F = 3.28$, $p = 0.080$). Neither playback treatment nor the interaction between playback treatment and prey mobility were significant factors in ANCOVAs, for latencies of any of the four predation stages ($p > 0.05$; detailed ANCOVA results in Table S1).

3.7. Squid alarm responses

We looked for potential effects of squids' engagement in hunting on their alarm responses to pile driving noise playbacks by comparing alarm response rates when the killifish was revealed and squid were pursuing it (Onset) to when the killifish was hidden (5min) at the beginning of playback. In Day Onset and Day 5min treatments, there were larger proportions of each of the four alarm response types during the first minute of the playback period compared to the pre-playback period (Fig. 8). Proportions of 'no response' were higher in the pre-playback period compared to the first minute of playback. In the Day 5min treatment, proportions of inking, jetting, startle, and body pattern change were significantly higher in the playback period ($p < 0.001$, $p < 0.001$, $p = 0.007$, and $p = 0.010$, respectively, Fisher's Exact tests; detailed statistics in Table S1). In Day Onset, only the proportion of jetting was significantly higher in the playback period ($p = 0.002$).

During the first minute of playback, a higher proportion of squid in Onset and 5min treatments showed alarm responses compared to Controls, and a higher proportion of squid had no response in the Controls (Fig. S2). In Day trials, there was a significantly lower proportion of squid with 'no response' in the 5min treatment compared to the Control treatment (OR = 0.05, 95% CI: 0.00–0.58, $p = 0.015$, Fisher's Exact tess), and there were no significant differences in any response type between Onset and 5min treatments. Pooling 5min and Onset treatments and comparing them with Controls, there were significant differences in the proportions of inking (OR = 9.60, 95% CI: 1.00–92.0, $p = 0.039$), jetting (OR = 10.50, 95% CI: 1.56–70.76, $p = 0.016$), and no response (OR = 0.10, 95% CI: 0.01–0.67, $p = 0.023$).

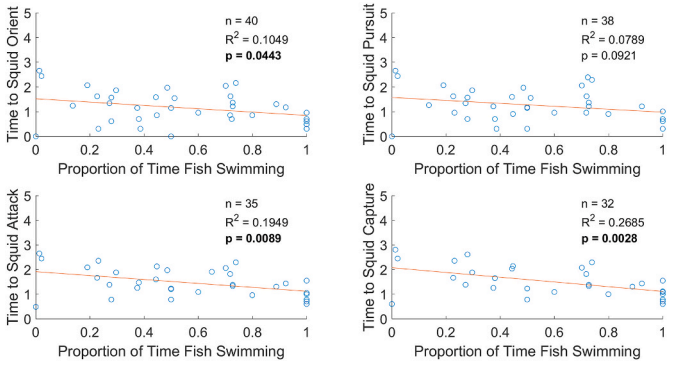

Fig. 7. Log-transformed time from fish reveal to the first occurrence of four squid predation behaviors (orient, pursuit, attack, and capture) plotted against the proportion of time the fish spent swimming prior to the predation behavior or the passing of 5 min, whichever occurred first. Data from all Day trials during which playback was started are presented here. Circles represent individual trials and lines are linear regression models. Significant p values ($p < 0.05$) are in bold. The transformation for the y-axis units was $\log_{10}(s+1)$, where s is time in seconds. In some trials, orient and pursuit occurred immediately upon prey reveal, thus time to these behaviors was assigned a value of 0 s.

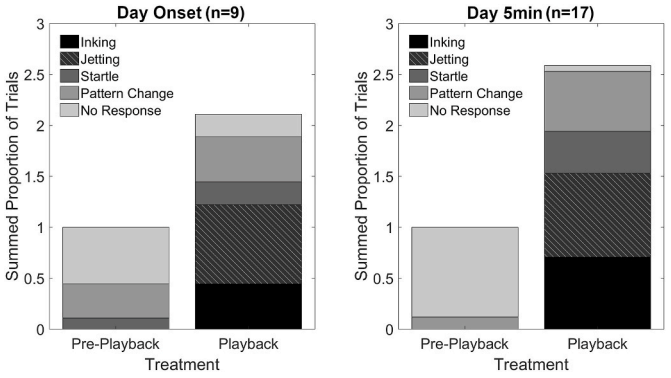

Fig. 8. Summed proportion of trials in which squid exhibited a type of alarm response, or no response, during the last minute of the pre-playback period ("Pre-Playback") and during the first minute (first 30 pulses) of pile driving playback ("Playback"), for the Day Onset (left plot) and Day 5min (right plot) treatments. Only trials for which data were available for 30 pulses are shown here (playback for several Onset and Control trials was stopped before 30 pulses elapsed because the squid had captured the fish). Proportions were found individually for each behavior category, which, aside from 'No Response', are not mutually exclusive. Therefore, summed proportions may exceed 1.

Alarm responses per pile driving impulse were analyzed for the first minute (30 impulses) of pile driving noise playback. The same patterns in alarm responses over time were observed in Day Onset trials, during which the squid was hunting at the start of playback, and Day 5min trials, during which the fish had not yet been revealed (Fig. 9). Squid displayed alarm responses at the highest rates within the first 5 pile driving impulses. Inking behaviors were extinguished first, followed by jetting and startle behaviors, with body pattern changes persisting the longest. Quasipoisson GLMs indicated that pile impulse number was a significant predictor of each of the four alarm response types ($p < 0.001$), and that noise treatment was a significant predictor of inking behaviors ($p < 0.001$; higher rate for 5min) jetting behaviors ($p < 0.05$; higher rate for Onset), and startle behaviors ($p < 0.001$) and not body pattern change behaviors ($p > 0.05$; detailed statistical results in Table S1). However, the low number of counts of inking behaviors and strong overlap in 95% confidence regions (not shown) for GLMs of each alarm response type suggest similar initial response rates on the first impulse and similar rates of decreased response over time between 5min and Onset trials. The reader is referred to Fig. S3 for a comparison of these data, per pile impulse, to the 1 min period just preceding the start of pile driving noise playback.

4. Discussion

Squid exposed to pile driving noise playbacks generally had lower prey capture rates, and squid were more likely to abandon pursuit of prey if noise started during their pursuit. Prey mobility significantly negatively correlated with squids' predation latency, whereas noise did not have a significant effect on predation latency. Squid exhibited similar alarm response rates during noise whether or not they were hunting at the start of noise. Together, these results suggest that pile driving noise seems to alter the feeding activity of squid and reduce squids' capacity to hunt. The extent, or duration of this has yet to be addressed. Similar to the distracted prey hypothesis, noise may shift squid predators' attention away from feeding tasks and toward the noise, which, given the observed alarm responses, appears to be perceived as a threat.

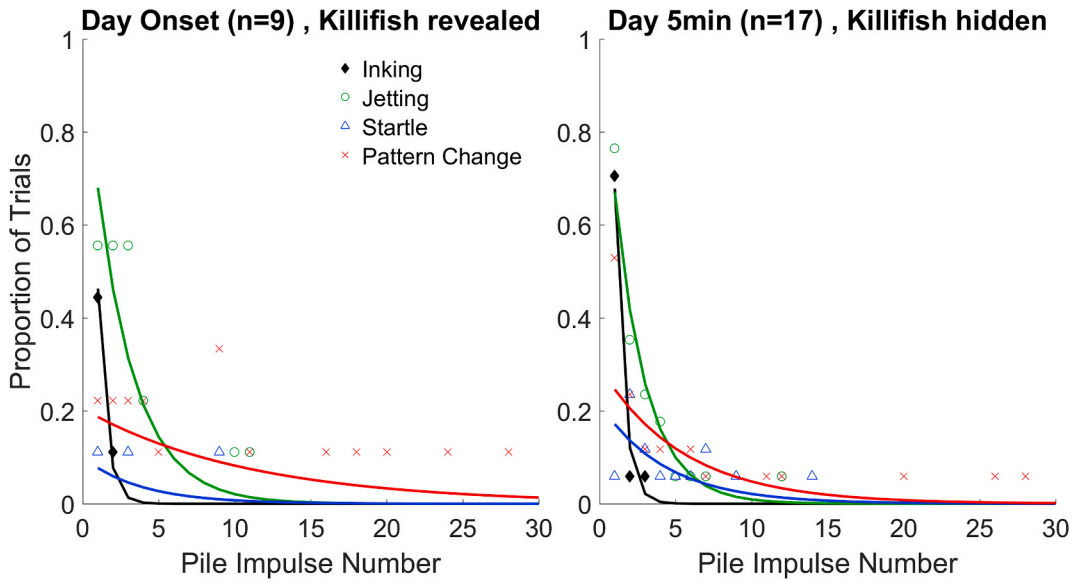

Fig. 9. Proportion of trials squid exhibited each type of alarm response, at each pile impulse number, for Day Onset (prey already released) and Day 5min (prey still hidden) trials. Each point in the scatterplot represents the proportion of trials in which a certain behavior occurred at that impulse number; solid lines of corresponding color are quasipoisson Generalized Linear Models (GLMs) for each response type. Only trials for which data were available for 30 pulses are shown here (playback for several Onset and Control trials was stopped before 30 pulses elapsed because the squid had captured the fish).

4.1. In-tank acoustic levels relative to hearing thresholds and in-situ acoustics

Though in-tank particle acceleration levels of the pile driving noise playback were spatially variable, they remained near or above physiological hearing thresholds for longfin squid at some frequencies, notably around 100–200 Hz. Along with the behavioral responses observed, this indicated squid were able to detect the noise playback. A comparison of the sound pressure spectra of in-tank pile driving noise with the killifish AEP data indicates that killifish were able to detect this noise at frequencies below 300 Hz. In this frequency range, amplitudes of the pile driving noise in the tank and in the field were higher compared to amplitudes at frequencies above 400 Hz,. Thus, as was the case with longfin squid, frequencies at which *F. heteroclitus* had highest sensitivities to sound overlapped with the frequency range at which pile driving noise tends to have highest energy.

The acceleration levels in the experimental tank exceeded those of the original file recorded in the field. This result is to be expected; the ratio between particle motion and sound pressure is typically increased underwater in tanks, relative to deep-water, free-field conditions (Campbell et al., 2019; Rogers et al., 2016). Careful calibrations of pressure and particle motion, as done in the present study, are needed for tank studies to address the acoustic conditions of this complex environment. The higher particle acceleration levels in the tank relative to the field recording (500 m horizontally away from a pile and 1 m above the seabed) suggest that $SAL_{z\text{-}pk}$ in the tank correspond to water-borne $SAL_{z\text{-}pk}$ expected within 500 m from the BIWF pile driving operation (Amaral et al., 2018). Though acoustic propagation in tanks differs from that in the field, the present study allowed a controlled environment and presentation of sound, and detailed, individual-based quantification of behavior. The present study indicates that at least playbacks of pile driving noise appear to disrupt squid engaged in feeding behaviors, and serves as a stepping-stone to inform related, future noise exposure studies in field conditions.

4.2. Prey capture rates

There were overall trends of lower proportions of squid capturing prey in noise treatments compared to controls. Importantly however, lack of statistical significance in differences of these proportions prevents conclusive interpretations, and larger sample sizes would aid assessment of whether noise exposure significantly reduces the likelihood of squid attempting to capture and successfully capturing prey. Additionally, Fisher's Exact tests, which were used in our study to compare low-count proportion data, are potentially limited in statistical power (Lydersen et al., 2009). Though different conditions of Night trials (lower temperatures, fall season instead of summer) prevented us from assessing diel influences on feeding behavior during noise, variability in capture rates indicates the potential for diverse responses to noise under different environmental conditions.

4.3. Failed predation attempts

In the Onset treatment, squid had significantly more failed attempts compared to other playback treatments. This suggests that if a sudden onset of impulsive noise, such as pile driving, occurs while squid are actively feeding, squid are more likely to miss opportunities for prey capture. Notably, squid confined to the experiment tank readily had the opportunity for multiple capture attempts, always remaining in close proximity to the killifish prey which could not escape. Wild squid may not have additional chances at capturing a particular prey item, e.g., if squid abandon a predation attempt and prey escape. Such reductions in the success rate of prey capture could lead to lower squid survival particularly when squid might be more resource-limited, for example in winter months when squid have been found to have slower growth rates and a higher incidence of empty stomachs (Macy, 1982; Vovk, 1985). Squid in the family Loliginidae, including longfin squid, have relatively high metabolic rates, fast digestion rates (4–6 h), limited energy storage, and need to eat little at once, but often (Bidder, 1950; Boyle and Rodhouse, 2005; Hanlon, 1990). Given this requirement of frequent feeding, if cessation of feeding during noise leads to longer-term reduced food intake, then the potential exists for population-level reductions in squid abundance. However, our study only addressed short-term impacts and we did not measure feeding behavior after noise exposure. As well, field pile driving operations occur for longer periods than in this study, up to several hours per day, though with variable noise (pile driving) and inter-noise (adjustment) periods (Amaral et al., 2018). Future studies should investigate chronic noise effects over longer exposures, and the

potential for long-term habituation, with respect to feeding behaviors. Longer-term, comparative field studies will be necessary to address hypotheses regarding chronic, ecological, and population level effects.

4.4. Alarm responses in feeding vs. non-feeding contexts

Squid that were hunting at the start of noise playback (Onset trials) and squid that had not yet encountered the fish at the start of noise playback (5min trials) had similar alarm response rates to the first several noise impulses, and similar habituation rates over repeated impulses. Thus, the presence of a fish and a squid's engagement in feeding behavior did not influence the squid's alarm response rates during noise. Initial alarm responses and habituation rates to noise were similar to those in a prior experiment on solitary squids placed in the same tank, without any other animals (Jones et al., 2020). While squid show the potential to habituate to pile driving noise quickly, the fact that the onset of noise can disrupt a hunting sequence means that squids' hunting could be disrupted when pile driving suddenly commences, potentially causing it to lose a meal each time a hunt is interrupted. Indeed, the results of these alarm behavior analyses likely explain why the squid in the Onset trials exhibited significantly higher rates of failed prey capture attempts.

4.5. Possible mechanisms driving behavior changes during noise

There are several potential mechanisms for the observed increase in squids' failed predation attempts, which could be investigated in future studies. These include: 1) 'distraction', or attention shifts, e.g. away from foraging behavior toward vigilance of potential predation threats, 2) increased stress which could arise via physiological changes and changes to behavioral motivation, 3) masking of hydrodynamic cues that might be utilized for detecting and accurately attacking prey, and 4) physical damage to squids' statocysts, which may detect acoustic cues, possibly including those resulting from prey movement.

Disruptions to foraging and feeding behaviors observed in the present study may be associated with 'distraction', i.e. attention shifts toward threat stimuli. This is suggested by the fact that in most Onset trials with failed predation attempts, squid immediately ceased pursuit at the start of noise playback and simultaneously jetted away, sometimes inking as well. These are known natural defense behaviors employed in response to perceived predator threats, suggesting squids' attention was diverted from a feeding task and toward predator defense. Across multiple taxa, animals have been found to reduce their foraging activity in the presence of potential threat cues (i.e. cues suggesting a predation threat), including acoustic cues (Chan and Blumstein, 2011; Dukas, 2002). For example, mud crabs (*Panopeus* spp.) in lab experiments significantly reduced their consumption rate of prey (clams) in the presence of played-back acoustic cues from predatory fish (Hughes et al., 2014). As evidenced by the occurrence of alarm responses in the present study, the 'attention shift' hypothesis appears to be a likely candidate mechanism for squids' cessation of feeding behaviors during noise. However, the other potential mechanisms described below cannot be ruled out.

We did not measure physiological variables such as changes in stress hormones or changes in respiration rate, which have been found in several noise-exposure studies on crabs and fish (Purser et al., 2016; Putland et al., 2019; Simpson et al., 2015 Wale et al., 2013b). Thus, physiologically-induced stress cannot at present be excluded as a potential mechanism behind reduced feeding behavior during noise.

Squid appear to utilize hydrodynamic cues from swimming predators to avoid being captured (York and Bartol, 2014; York et al., 2016), and, as suggested in cuttlefish (Komak et al., 2005), possibly utilize similar cues from prey to aid in making accurate attacks on prey. The presence of rows of hair cells (called the "lateral line analog") observed along the head and arms of cuttlefish and squid suggests that such a function may exist (Budelmann and Bleckmann, 1988). Fish are known to utilize hydrodynamic cues detected by their lateral line in order to find prey (Coombs and Braun, 2003). Although the ecological relevance of these available hydrodynamic cues to cephalopods remains unclear, water motion in noisy acoustic fields could in theory mask (i.e. prevent squids' detection and utilization of) hydrodynamic cues from prey, as has been suggested for fish (Mogdans, 2019). In the present study, this effect would be expected to contribute to the failed (i.e. missed) attacks observed, rather than the failed (i.e. abandoned) pursuits observed.

Some studies (e.g., Solé et al., 2017, 2018) have reported physical damage of sensory structures and hair cells in cephalopods' statocysts and lateral line analogs after animals were exposed to long (2 h) continuous acoustic stimuli (sinusoidal frequency-modulated sweeps). Yet comparatively in fish, impacts on auditory structures were limited or absent for fish exposed to pile driving sounds, which were higher intensity than those used in the present study (Casper et al., 2013b). Indeed, though physical statocyst damage cannot be fully discounted, with the lack of comparative anatomical studies at shorter presentations (<10 min in this study), such damage may be less likely in our study.

4.6. Comparisons with other taxa

Only a handful of published studies have investigated the influences of noise on invertebrates' feeding behavior. A playback experiment with shore crabs (*Carcinus maenas*) found that if ship noise was played once crabs had found food and started feeding, they were more likely to cease feeding (Wale et al., 2013a). Similarly, squid in the present study often ceased pursuit of prey if noise was started during their predation sequence. Filter-feeding blue mussels (*Mytilus edulis*) increased their clearing rate during pile driving relative to ambient sound conditions, suggesting an increased feeding rate and metabolic demand during noise (Spiga et al., 2016). Mussels (*M. edulis*) have also responded to in-tank substrate vibrations by partially closing their valves, which could potentially lead to changes in food intake and respiration (Roberts et al., 2015). Natural noise (running water from a river) reduced maximum feeding rate and significantly reduced prey handling time in freshwater damselfly larvae (*Ischnura elegans*) feeding on *Daphnia* sp. (Villalobos et al., 2017). Thus, several studies have suggested negative effects of both anthropogenic and natural noise on feeding behaviors of aquatic invertebrates. Yet, noise impacts are only beginning to be investigated in these diverse taxa.

Few studies have investigated effects on noise on feeding and foraging behavior of fish as well. Because squid occupy similar trophic niches to many predatory fish (Boyle and Rodhouse, 2005), such comparisons are useful to provide context, given the limited comparative cephalopod data available. Three-spined sticklebacks (*Gasterosteus aculeatus*) exposed to white noise had significantly higher food discrimination error and food-handling error when attempting to feed on *Daphnia* sp. prey (Purser and Radford, 2011). Captive cichlids (*Amatitlania nigrofasciata*) significantly decreased foraging behavior, in terms of number of pecks and number of individuals foraging, during boat noise (McLaughlin and Kunk, 2015). In a field-study, captive roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*) made significantly fewer feeding attempts when exposed to noise from an actual boat motor (Magnhagen et al., 2017). Thus, like the present study with squid, multiple studies on fish have demonstrated reductions in feeding and foraging activity, and under a variety of noise conditions. These studies further demonstrate that a variety of variables pertaining to feeding behavior, such as quantity of food intake, capture rates, and time spent foraging, can be altered during noise, emphasizing the importance of quantifying multiple variables that may lead to changes in the amount or rate of energy intake.

5. Conclusions

The present study uniquely demonstrates how pile driving noise can alter the feeding behavior of squid. To the authors' knowledge, this

study is the first to demonstrate changes in feeding behaviors of cephalopods during anthropogenic noise. These data underscore the importance of accounting for behavior of both predator and prey species, and for ecosystem dynamics, when assessing noise effects. Squid were significantly more likely to abandon pursuit of prey and have failed capture attempts when noise playback started during squids' predation sequences. In addition, a lower proportion of squid captured live killifish prey in noise exposure trials compared to silent Control trials, though these differences were not statistically significant. Missed opportunities for prey capture and lower feeding rates during anthropogenic noise could lead to reductions in growth or survival of individuals, particularly for longfin squid, with their high-metabolic rates that require frequent feeding; this could be especially damaging to squid survival when prey resources are limited. Future work should address the potential longer term metabolic consequences of noise exposure. Squids' latency to capture prey was significantly negatively correlated with fish locomotion, emphasizing the importance of considering natural covariates at play when investigating effects of anthropogenic stressors on predator-prey relationships. Further, at the onset of noise exposure, when squid were engaged in hunting they had similar alarm response rates compared to when they were not hunting; this indicated that both in feeding and non-feeding contexts, individual squid were similarly alert to threat stimuli. Changes in feeding behaviors reported here have potential implications for reduced feeding activity of squid exposed to construction noise of marine pile driving operations. However, behaviors and acoustics observed in the laboratory may differ from those *in situ*. Thus, future comparative field studies are needed to further investigate influences of pile driving noise on foraging behaviors of squid. Further, the present results raise questions regarding how other key longfin squid behaviors such as breeding, shoaling, predator avoidance, and habitat selection may be impacted by noise.

CRediT authorship contribution statement

Ian T. Jones: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **James F. Peyla:** Methodology, Investigation, Writing - review & editing. **Hadley Clark:** Methodology, Investigation, Writing - review & editing. **Zhongchang Song:** Investigation, Writing - review & editing. **Jenni A. Stanley:** Conceptualization, Investigation, Writing - review & editing, Supervision, Funding acquisition. **T. Aran Mooney:** Conceptualization, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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